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Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested

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With 6 figures

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1. Introduction

In the wet savannahs of Lamto (Ivory Coast), as in most of the herbaceous humid tropical environments, invertebrate communities in the soil are largely dominated by geophagous species (termites and chiefly earthworms) which feed on the organic matter accumulated in soil: they represent from 52.5 to 77 % of the biomass, according to the type of savannah (Athias *et al.*, 1975; Lavelle, 1983; Lavelle *et al.*, 1981). The consumers of litter are rarely abundant, except when the shrub cover is dense (38.5 % in the unburned savannah densely stocked with shrubby trees). As to the rhizophagous species, they do not amount to more than 0.3 % of the biomass.

The mean annual population density of the geophagous earthworm *Millsonia anomala* Omodeo populations varies from 90,000 to 229,000 per ha and their biomass from 72 to 241 kg $\times$ ha^{-1}. This worm indiscriminately ingests soil from the top 10–15 cm of the profile. The total consumption by this species reaches 500 Mg $\times$ ha^{-1} $\times$ a^{-1} and that of the whole earthworm community 1,000 to 1,200 Mg. Yearly 15 Mg $\times$ ha^{-1} organic matter passes through the digestive tracts of the earthworms, representing a third of the reserves accumulated in a herbaceous savannah and 60 % of the organic matter in the first 10 cm, biotically the most active part of the soil (Lavelle, 1978).

Experiments were undertaken, to determine how the worms exploit a resource apparently as poor as this organic matter, and to evaluate the consequences of this utilisation for the dynamics of humic reserves. A preliminary study, which compared the nutritive value of soil, taken at different depths, to 3 species of geophagous worms, had shown that it is the quality and not only the quantity of organic matter which determines the growth of the worms, and this differently according to the species (Sow, 1979; Lavelle *et al.*, 1980). Further work showed the importance of the hydrosoluble organic matter fractions on the growth of the worms and the mechanisms of their interactions with the soil microflora (Lavelle *et al.*, 1983; Zaidi, 1985).

In the present study, young *Millsonia anomala* were fed with a soil poor in organic matter but supplemented with plant materials of different origin (roots or leaves), decomposed under aerobic or anaerobic conditions during periods of different length (0, 2, 5 or 10 weeks) at 27 °C. The objectives were to understand better on which precise organic matter fractions this worm was feeding to explain why it shuns dead roots and to propose some new hypothesis on the influence exerted by these animals on the roughly 15 Mg of organic matter per ha which pass through their digestive tracts every year.

The response of the worms to different organic materials has been evaluated by way of their total consumption, their growth rate and their growth efficiency, under approximately optimal conditions of temperature and humidity.

2. Materials and methods

2.1. Culture of the worms

The young *M. anomala* taken from a shrubby savannah soil were raised by the method of Lavelle, 1975, which allows for a measurement of the soil consumption and of the growth of the worms. The organic materials described below were added at a rate of 1 % to the soil of the 10–25 cm depth from a savannah sparsely stocked with trees,

containing 1.2 % of organic matter. For each of the 14 powdered samples tested and the soil blank, 2 repetitions were done. Each of the 2 cultures was made up of a Petri box with 725 g of soil and 5 young worms aged 1 to 4 weeks whose gross mass varied from 40 to 100 mg. The examination of the cultures was done every 7 d during 70 d.

At each time interval, the mass of the worms[1] and their soil consumption (C) were measured, which allowed calculation of their mean daily growth ($m \% \times d^{-1}$), their relative mean consumption ($g\ C \times g^{-1}\ m_s$ soil ingested $\times g^{-1}\ m_b$ of fresh mass $\times d^{-1}$) and their growth yield or efficiency $E = m \% \times d^{-1}$ divided by c, where c is the amount of organic matter ingested daily per g of fresh mass (m_b) of worms.

2.2. Nature of the substrates

The roots and the leaves of *Loudetia simplex*, the dominant Graminea of grass savannas at Lamto, were allowed to decompose separately either under aerobiosis, or under anaerobiosis over 2, 5 and 10 weeks. Thus were prepared 14 series of different plant materials:

Leaf material

L_0 Aerobiosis:	L_2A – L_5A – $L_{10}A$
Anaerobiosis:	L_2An – L_5An – $L_{10}An$

Root material

R_0 Aerobiosis:	R_2A – R_5A – $R_{10}A$
Anaerobiosis:	R_2N – R_5N – $R_{10}N$

time of decomposition (in weeks)

The chemical composition of fresh and decaying plant materials was determined by JARRIGE's method (1961) which separates the organic matter into 7 fractions: first hydrosoluble fraction (H_1), lipids, second hydrosoluble fraction (H_2) occluded by the lipids, hemicelluloses, cellulose, lignin and ashes. The separation of these fractions is brought about by hydrolysis of increasing strength. Their energetical value is measured by estimation of the hydrocarbons, extracted at each analytical step, by the HAGEDORN & JENSEN (1923) micromethod.

3. Results

3.1. Analysis of the organic matter

The results of these assays indicate the following general contrasting trends between leaves and roots:

– the undecomposed material: the fresh leaves (L_0) are higher in H_1, lipid, hemicellulose and cellulose content than the fresh roots (R_0) which in turn are conspicuous by their high lignin and H_2 content (fig. 1);

– the decomposing materials: the treatment (aerobiosis/anaerobiosis) exerts in general more influence on the roots than on the leaves. The decomposition of the roots is slower than that of the leaves. However, the process is accelerated under anoxybiosis (fig. 1).

– Decomposing roots show more lignin, cellulose and H_2 than decomposing leaves. The lipid content of the decomposing roots increases along the sequence of humification, most markedly under anaerobiosis (fig. 1).

– All of the decomposing leaves have a high content of hemicellulose. The other fractions, hydrosolubles 1, lipids, hydrosolubles 2 and cellulose undergo a degradation in leaves which progresses with decomposition.

– The reducing power of the fraction H_1 and cellulose, which is consistent with the energetical capacity of these substrates, is in general higher for the leaves than for the roots (fig. 2). A reverse situation is observed for H_2 although the reducing power per unit of substrate is lower.

[1] Their gross biomass (m_b) includes gut content.

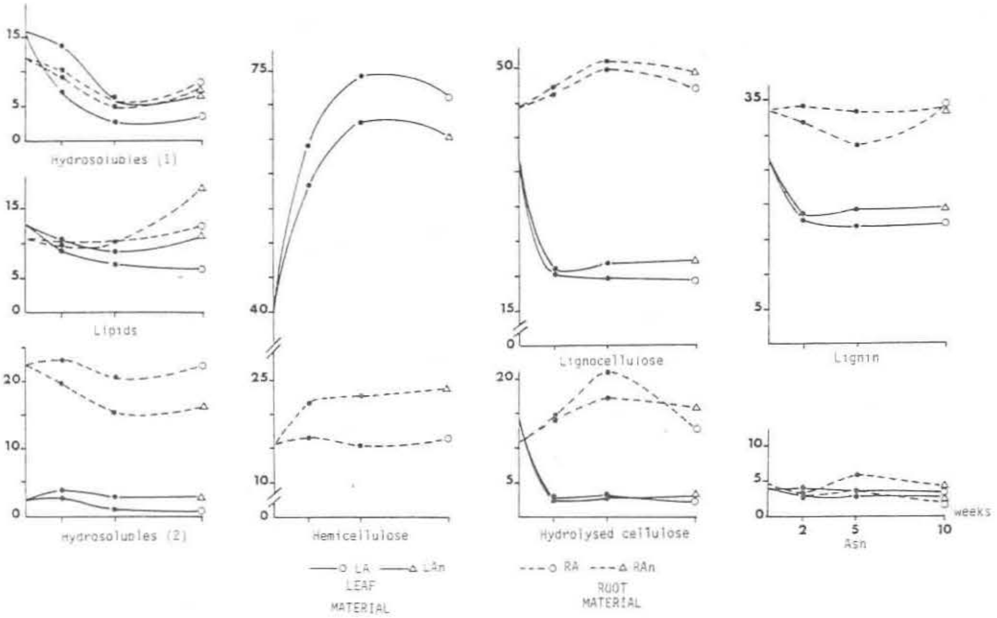

Fig. 1. The various components of decomposing leaves (L) and roots (R): a comparison of evolution when undergoing aerobic (A) or anaerobic (An) decomposition ($g \times 100\ g^{-1}$); lipids: $mg \times 100\ g^{-1}$.

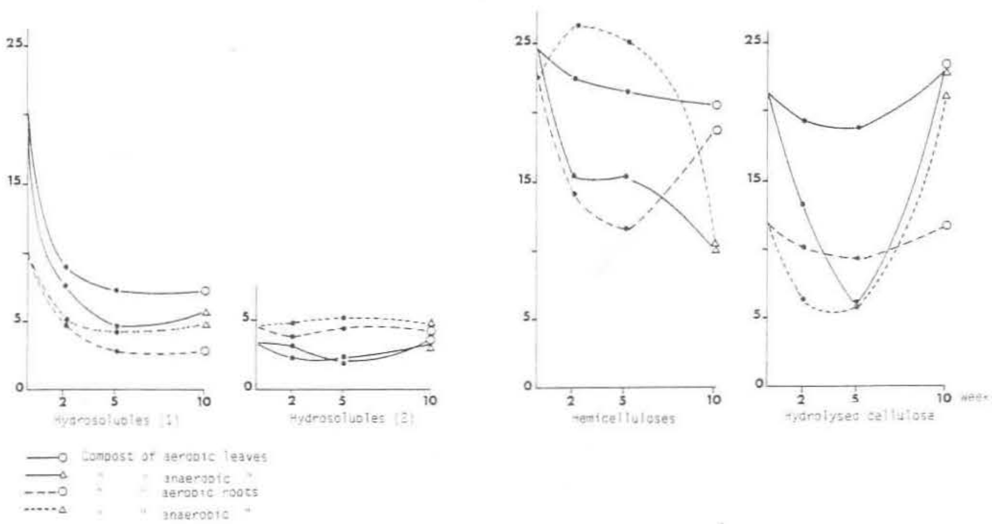

Fig. 2. Reducing power of decomposing leaves and roots (in mg eq. glucose $\times 100\ g^{-1}$).

3..2. The cultures

The consumption of non-enriched soil (S) by the worms is high ($18\ g\ m_x$ soil $\times g^{-1}\ m_b \times d^{-1}$) while their growth, by contrast is relatively slow ($1.93\,\% \times d^{-1}$) and the growth yield is 8.1 (fig. 3).

The worms fed with soil enriched in powdered leaves (L_0) consume less ($10.7\ g\ m_x \times g^{-1}\ m_b \times d^{-1}$) than those fed with blank soil (S), whereas their growth rate is improved (4.14%) and their growth yield is double (16.6%; fig. 3).

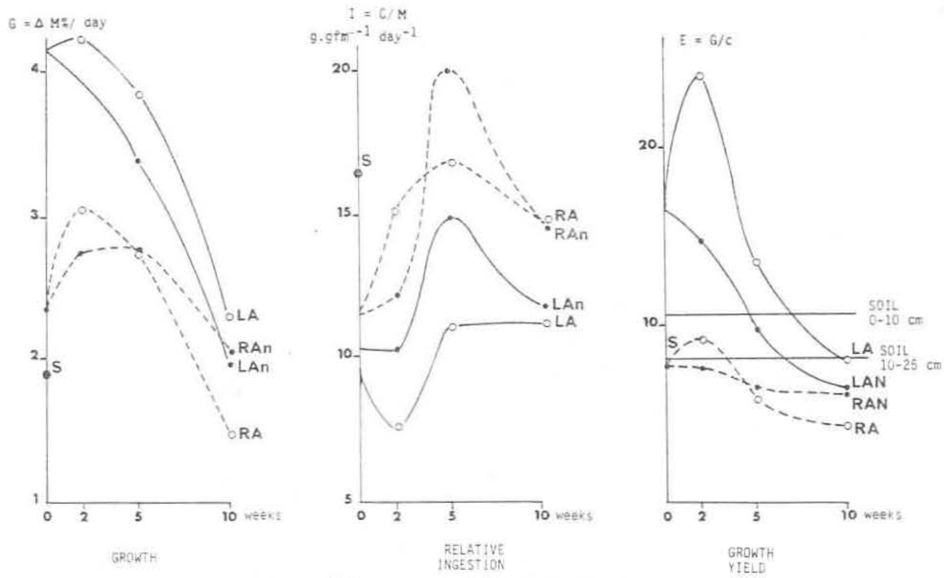

Fig. 3. Growth, relative ingestion and growth yield of earthworms cultured in soil amended with decomposing leaves (LA: aerobic, LAn: anaerobic) and roots (RA, RAn). M: mass in g.fm; I: daily soil ingestion in g; c: organic matter ingested in $g \times d^{-1}$.

In the presence of decomposing leaves, either aerobic or anaerobic, the soil consumption is less than with the blank soil (S). The growth is improved, and with equal times of decomposition the consumption is less and growth faster for aerobically compared with anaerobically decomposed leaf material. It is with the 2 weeks aerobic plant material that one sees the largest decrease in soil consumption ($7.6\ g\ m_s \times g^{-1}\ m_h \times d^{-1}$) and the highest growth rate (4.26%).

The growth efficiency, low with the blank soil (S), 8.1, is enhanced by a factor of 2 when the soil is enriched with undecomposed leaf powder (L_0): 16.6, and by 3 with 2 weeks aerobic decomposition (L_2A): 24.1. Then it decreases with the length of decomposition. Those anaerobic leaf material cultures yield a growth efficiency lower than the aerobic ones, but higher than the blank (fig. 3).

The undecomposed root powder (R_0), in contrast to the leaf powder (L_0), accelerates little the growth of the worms ($2.33\% \times d^{-1}$) which is only slightly greater than that obtained with the blank soil (1.93%; fig. 3).

Decomposition of root material improves somewhat the growth rate of the worms, in comparison with the soil blank, but the soil consumption is high and the growth yield lower than that of the blank, except for the R_2A material. Earthworms fed soil with higher organic content of the upper 10 cm, had a growth yield of 10.5, greater than that obtained with any root material or 10 weeks decomposed leaf material.

4. Discussion

4.1. Response of earthworms to organic matter type

If one compares the effect of the different substrates to that of the soil organic matter, 6 substrates among 14 yield a growth efficiency clearly lower than that obtained with the nutrient-poor soil (1.2% organic matter) of the 10–25 cm level. Of the root materials, only R_2A improved the growth yield of earthworms (fig. 3). The root material, in general, is a poor food for *Millsonia anomala*. It is only when it is already well decomposed, during 2 to 5 weeks, mainly under anaerobiosis, that it becomes somewhat more available to the worm.

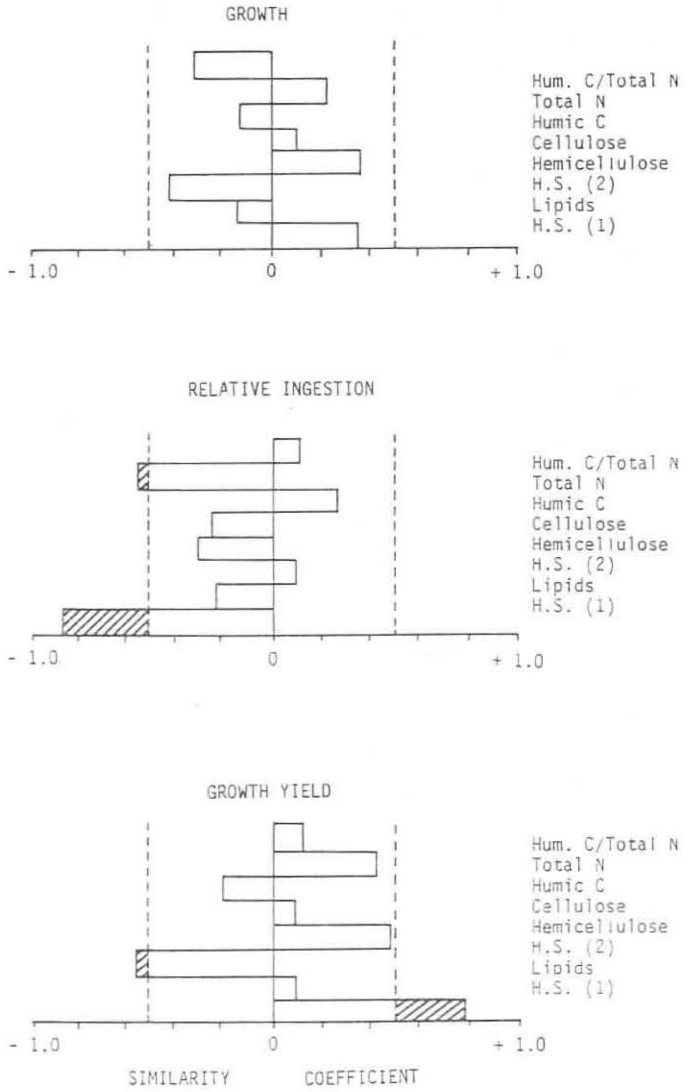

Fig. 4. Similarities between the different organic fractions and nitrogen in decomposing material and the biological parameters of *Millsonia anomala*. Values greater than 0.50 are indicated by shading.

The foliar material, by contrast, in equal amounts accelerates the growth of the young worms. When decomposed over 14 d under aerobic conditions it becomes an exceptional food source. However, it appears that a long decomposition period decreases its nutritive value. There is clearly an inverse relationship between the nutritive value of the food materials and the amount consumed by the worms. Consumption must be regulated in relation to the quality of the ingested soil, i.e. by the form of the organic matter.

For this reason, different chemical classes of the organic materials supplied as food have been examined separately. Differences between organic materials in both chemical nature and the worm's response to them (measured as consumption, growth and growth yield) are more marked in

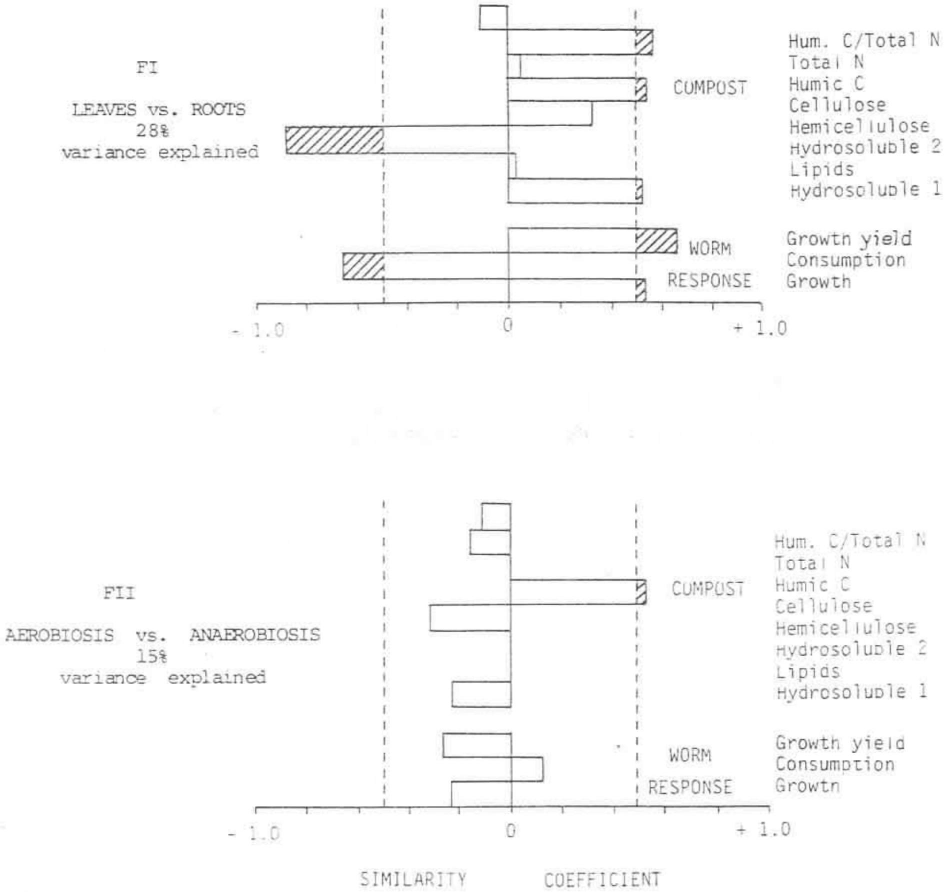

Fig. 5. Similarities between factors and variables.

relation to origin (leaf or root) than treatment during decomposition (aerobic or anaerobic), the chief chemical differences being in their content of watersoluble fractions H_1 and H_2, cellulose and total nitrogen (figs. 3 and 4).

4.2. Response of earthworms to the quality of organic matter

Similarities (as calculated by the Gowers's index) between the different components of the organic materials and the biological parameters of *Millsonia anomala* show that the consumption by the worm is inversely related to the hydrosoluble fraction 1 and to total nitrogen. The growth yield is positively related to hydrosoluble 1 and negatively to H_2 (fig. 4).

Principal components analysis of the data (programme Constel, MEYER, 1974) has led to the isolation of 2 essential factors. The first separates leaves from roots and the second, the treatment received by these materials, i.e., aerobiosis and anaerobiosis (fig. 5).

The calculated similarities between these 2 factors and the different variables show that the first factor FI, which expresses 28 % of the variance, is correlated negatively with hydrosoluble 2 and with soil ingestion by the worm. It shows high positive similarities with the following parameters: total nitrogen, cellulose, hydrosoluble 1, growth and growth yield of the worm. The second factor,

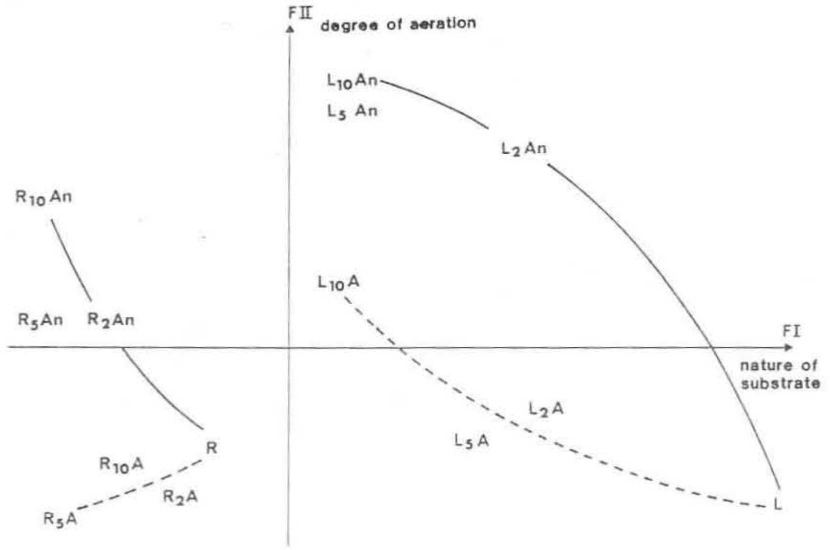

Fig. 6. Position of the different stages of metabolic evolution of two substrates, in the plane of the factorial axes I and II.

FII, which represents 15 % of the information is positively correlated with the cellulose. It separates aerobiosis from anaerobiosis.

The different organic materials form 2 large groups on the basis of their coordinates in the space of the 2 factors FI and FII: leaves on one side, and roots on the other. Within these groups, one sees a divergence between aerobically and anaerobically decomposed materials (fig. 6).

5. Conclusion

The large variability of the worms' response to the different types of organic matter confirms the importance to them of its quality. It has been shown that the easily assimilable hydrosoluble organic matter (the hydrosoluble "1" fraction) favours growth with decreased soil consumption, and consequently reduced energy expenditure of the earthworms (LAVELLE, ZAIDI & SCHAEFER, 1983). The nitrogen content of organic matter exerts a similar effect, whereas certain compounds, possibly toxic, of the hydrosolubles "2" category and more generally the recalcitrant compounds of the lignocellulose fraction, exhibit an inverse effect. The composition of the organic matter is therefore an important factor in the regulation of the earthworm's activity, and above all of the microbial activity induced in the casts, whose mid-term effect on the dynamics of organic reserves is important. In general, one may conclude that the worms' mechanical activity and the induced microbial activity in the casts are favoured in the presence of low quality nutritive resources (in the sense of SWIFT *et al.*, 1979).

Considering the strategies of organic matter recycling within the ecosystem (*sensu* COLEMAN *et al.*, 1983), the fact that the organic matter of the first 10 cm of soil is a better food than root material, fresh or decomposed, is of great interest. The low nutritive quality of root material may be considered as a possible defence mechanism against consumers. Moreover, the distribution of these roots in the soil body and the presence in the rhizosphere of an abundant and diversified microflora do not make the mechanical and disseminating action of the soil fauna as indispensable as for the epigeous litter. It seems, then, that this root material is transformed directly by the microflora into humic matter resistant to decomposition, without significant macrofaunal action. This organic matter exhibits a very low mineralization rate, from 1 to 2 % per week under standard

laboratory conditions (soil dried, sieved to 2 mm, rehumidified to pF 2.5) (SCHAEFER, 1974; DARICI *et al.*, 1987). The activation of this mineralization and the release of nutrients from root debris are stimulated in these savannahs by biotical activity. Readily assimilable organic compounds are released into the environment in the form of root exudates, or of earthworm cutaneous and intestinal mucus, and in a more general way, earthworms improve the conditions of microbial activity (soil moisture, transport, lifting of antibiosis and priming) and of access to organic resources through removal of physical protections (LAVELLE, 1984; BAROIS & LAVELLE, 1986).

The microflora, thus activated, becomes capable of mineralizing the recalcitrant organic matter. This aptitude, nevertheless, varies according to climatic conditions and the precise state of the organic reserves. One may then postulate that the liberation of the nutrients thus brought about is in harmonious balance with the needs of the plants whose activity undergoes the same variation in relation to climate.

These results, lastly, lead us to question, at least in these humid savannahs, the proper grounding of theories and recent models which relate the "resistance" of organic materials to their age (see for example VAN VEEN & PAUL, 1981; PARTON *et al.*, 1987). Future research ought to examine whether all of the organic soil fractions are digested by geophagous earthworms, independently of their degree of resistance (or of their "age"), or only less resistant fractions and short lived targets.

6. Acknowledgements

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7. Résumé · Resumen

[Consommation de terre et croissance de *Millsonia anomala*, un ver de terre tropical: influence de la qualité de la matière organique ingérée]

Dans la savane de Lamto (Côte d'Ivoire), les populations de vers de terre abondent, leur consommation annuelle de terre impressionne (1000 à 1200 Mg × ha^{-1}). Ainsi, une quantité appréciable de matière organique du sol passe par leur tube digestif par an: 60% de la matière organique totale du niveau 0–10 cm.

Les essais réalisés ont pour but de savoir comment les vers tirent parti d'une ressource aussi pauvre quest le sol de ces savanes (1.2% de matière organique en moyenne).

Aux fins de préciser quelles sont les différentes fractions qui entrent dans l'alimentation de ces vers, l'espèce la plus commune (*Millsonia anomala* OMODEO) a été élevée dans des substrats enrichis en matière organique de différente qualité (composts). Les divers critères de réponse des vers (consommation, croissance, rendement de croissance) aux enrichissements appliqués conduisent à postuler une régulation de l'ingestion de terre par les vers en fonction de la qualité du sol.

Cette étude confirme les hypothèses de travaux antérieurs: affinité entre la consommation des vers et l'activité de la microflore associée à la matière organique, ou bien encore, rôle de certains extraits hydrosolubles dans la régulation de l'intensité de l'activité mécanique des vers.

Au total, l'ensemble des résultats obtenus conduit à mieux comprendre le fonctionnement des populations de vers dans un sol de savane. Ils ouvrent de multiples voies de recherche, orientées vers la digestion de matière organique par les vers géophages.

[Ingestion de tierra y crecimiento de *Millsonia anomala*, una lumbriz de tierra tropical: influencia de la calidad de la materia orgánica ingerida]

En la sabana de Lamto (Costa de Marfil), las poblaciones de lumbrices son abundantes, y su consumo anual de tierra es impresionante (1000–1200 Mg × ha^{-1}). Asi, una notable cantidad de materia orgánica del suelo pasa anualmente por su tubo digestivo: 60% de la materia orgánica total del nivel 0–10 cm.

Los ensayos realizados tienen por meta, saber como las lumbrices explotan un recurso tan pobre como lo es el suelo de estas sabanas (1.2% de materia orgánica en promedio).

Con el fin de conocer cuales son las diferentes fracciones que entran en el regimen alimenticio de estas lumbrices, la especie más común (*Millsonia anomala* OMODEO) ha sido criada en sustratos enriquecidos en materia orgánica de

diferente calidad. Los diversos criterios de respuesta de las lumbrices (consumo, crecimiento, rendimiento de crecimiento) a los enriquecimientos aplicados conducen a conceptuar una regulación de la ingestión de tierra por las lumbrices en funcion de la calidad del suelo.

Este estudio confirma las hipótesis de trabajos anteriores: afinidad entre el consumo de las lumbrices y la actividad de la microflora asociada con la materia orgánica, o además, papel de ciertos extractos hidrosolubles en la regulacion de la intensidad de la actividad mecánica de las lumbrices.

Al total, el conjunto de resultados obtenidos conduce a entender mejor el funcionamiento de las poblaciones de lumbrices en el ambiente sabana. Ellos abren numerosas vias de investigación, orientadas hacia la digestión de materia orgánica por lombrices de tierra geófagas.

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In the Lamto savannah (Ivory Coast), the earthworm communities are very large and their annual ingestion of soil is impressive (1,000 to 1,200 Mg × ha^{-1}). Thus a significant amount of soil organic matter is annually consumed: 60% of the total organic matter of the 0–10 cm level.

The investigation undertaken examined how the worms exploit a resource as poor as the soil of these savannahs (1.2% organic matter). To discover which of the different organic fractions enter the diet of the worms, the most common species (*Millsonia anomala*) was reared in substrates enriched in organic matter of different quality. The various aspects of the worms' response (consumption, growth and growth yield) to the enrichments applied, have led us to postulate a regulation of the soil ingestion by the worms as a function of the quality of organic matter.

This study confirms the hypothesis formulated from earlier research that there is an affinity between the worms' consumption and the activity of the microflora bound to organic matter, and moreover, supports the conclusion that certain water-soluble extracts regulate the intensity of earthworm mechanical activity.

In general, this investigation leads to an improved understanding of the functioning of the worm populations in a savannah environment. It opens up several lines of research related to the digestion of organic matter by geophagous worms.

Key words: Tropical savannah, soil, organic matter, ingestion, earthworm, *Millsonia anomala* OMODEO, Acanthodrilidae, Oligochaeta, metabolism, biotic activity, interaction, microorganisms.

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